Early–Middle Frasnian cyrtospiriferid brachiopods from the East European Platform

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The cyrtospiriferids are among the most important fossils in the Frasnian strata of the East European Platform (EEP). During the Early Frasnian (*Palmatolepis falsiovalis* Zone) the numerous and morphologically distinct Uchtospiriferinae, accompanied by very scarce Cyrtospiriferinae, are known from South Timan. The mass appearance of cyrtospiriferins on the platform at the beginning of the Middle Frasnian is linked with significant sea-level rise of Devonian Transgression-Regression (T-R) cycle IIc. At that interval these brachiopods attain their highest diversity of the entire Frasnian. The Early Frasnian type species of the genus *Uchtospirifer* is here revised, and subfamily Uchtospiriferinae re-established. *Cyrtospirifer schelonicus*, *C. rudkinensis*, *C. mylaensis* sp. nov., and *C. tenticulum* are described from the Middle Frasnian of NW and central regions of EEP and Middle Timan.

Key words: Brachiopoda, Cyrtospiriferidae, Early–Middle Frasnian, East European Platform, Timan, Russia.

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Introduction

Proliferation of members of the Family Cyrtospiriferidae is probably the most distinctive feature of the Late Devonian brachiopod faunas of the East European Platform. The earliest record on the occurrence of these brachiopods in European Russia can be found in the publication by Verneuil (1845). In *Géologie de la Russie d'Europe et des montagnes de l'Oural* he described a number of Devonian brachiopod taxa including *Spirifer disjunctus*, a species originally described by Sowerby (in Sedgwick and Murchison 1840) from the Late Devonian of England, and a new species *Spirifer tenticulum*. Later, Venyukov (1886) and Obrouchev (1916) completed more comprehensive studies of spiriferid brachiopods from the north-western (Main Devonian Field) and central (Central Devonian Field) regions of Russia (Fig. 1), followed by important publications by Nalivkin (1941) and Ljaschenko (1959, 1973).

By contrast, the Late Devonian brachiopods from the Middle Timan region have not been described, although an extensive brachiopod collection from the region sampled by Chernyshev in the late nineteenth century is still housed in the Academician F.N. Chernyshev Central Scientific Geological and Prospecting Museum, St. Petersburg. This collection is an important source of the brachiopod specimens for the present study.

The objective of this paper is to study major patterns of brachiopod faunal dynamics in the mid-Frasnian of the East European Platform and their correlation with sea-level fluctuations. Taxonomic revision of some cyrtospiriferid species is proposed. Detailed information on the Upper Devonian geology and stratigraphy of the studied sections can be found in publications by Hecker (1941), Ljaschenko (1959, 1973), Sorokin (1978), Yudina et al. (1997), Zhuravlev et al. (1997, 2006) and Oleneva (2003).

Institutional abbreviation.—CNIGR, The Academician F.N. Chernyshev Central Scientific Geological and Prospecting Museum, St. Petersburg, Russia.

Other abbreviations.—EEP, the East European Platform; T-R, transgressive-regressive (cycle).

Regional setting and stratigraphic remarks

The oldest species of *Cyrtospirifer* reported from the East European Platform are *Cyrtospirifer echinosus* Ljaschenko, 1958 and *C. sublimis* Ljaschenko, 1973 from the Timan Horizon of the South Timan (Ljashenko 1973). Quantitatively, they were minor components of the Early Frasnian brachiopod associations typically dominated by *Uchtospirifer* (Fig. 2). Immigration of brachiopods of the subfamily Uchtospiriferinae into the South Timan, Volga-Ural area, Urals and central regions of the East European Platform occurred during the initial transgressive phase of T-R cycle IIb of Johnson et al. (1985), designated as Devonian T-R cycle

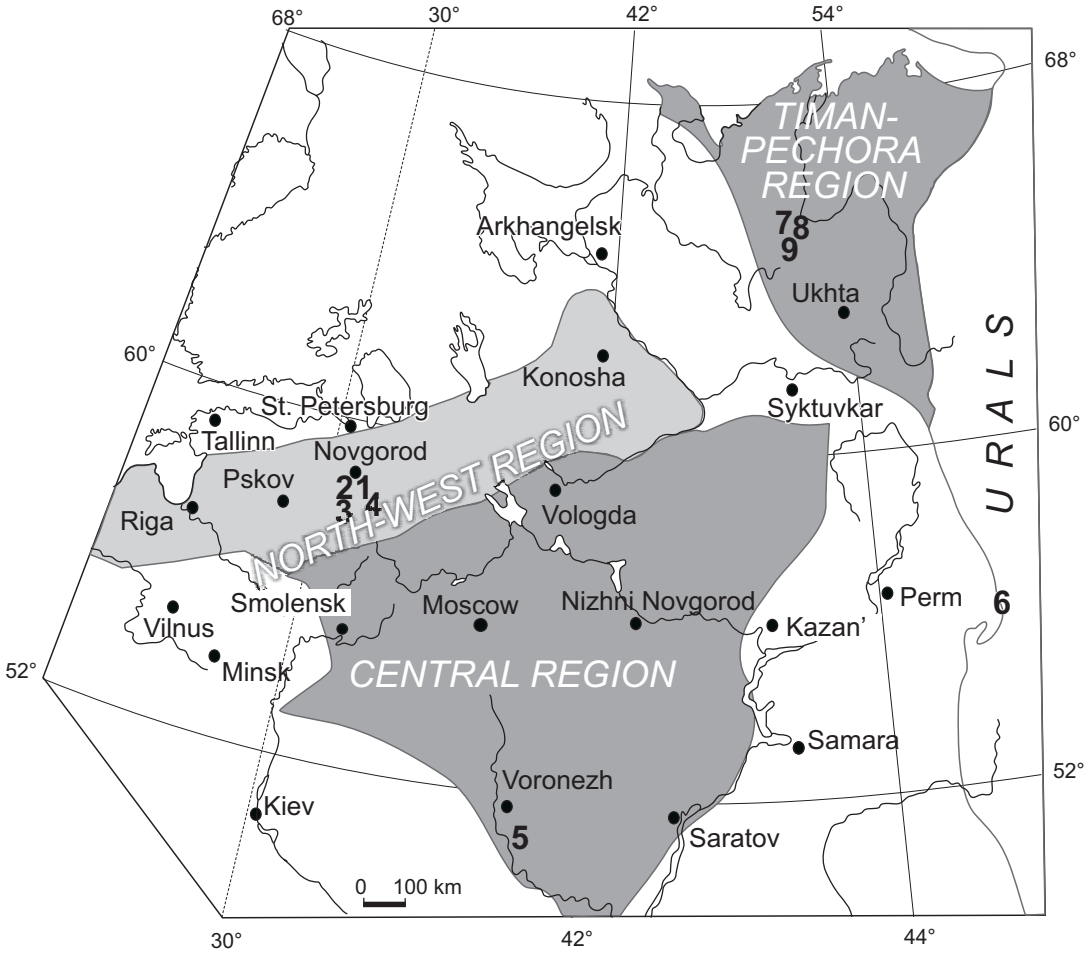

Fig. 1. A map showing the position of Frasnian brachiopod localities containing cyrtospiriferids of the East European Platform. Abbreviations: 1, Il'men Lake; 2, Schelon river; 3, Koloschka river; 4, Psizha river; 5, Rudkino village; 6, Kyn village; 7, Myla river; 8, Tsylma river; 9, Pizhma Pechorskaya river.

IIb-1 by Day (1996). This stratigraphic interval corresponds to the lower part of the *Palmatolepis falsiovalis* Zone (Rzhonsnitskaya 2000; Fig. 2). Uchtospiriferines became increasingly abundant in the upper part of the Timan Horizon. The horizon represents a period of sea-level high stand that continued into the Sargaevo Horizon (House et al. 2000). However, uchtospiriferines disappeared by the end of the Timan time (upper part of the *Pa. falsiovalis* Zone, within lower Montagne Noire Zone 4 of Klapper, 1989). The succeeding brachiopod associations of the Sargaevo Horizon (*Pa. transitans* Zone; see Rzhonsnitskaya 2000) includes abundant rhynchonellids, atrypids, and spiriferids (*Eleutherokomma*). Appearance of that fauna was mainly correlated with the T-R cycle IIb/c (Racki 1993) coinciding to Euramerican Devonian T-R cycle IIb-3 by Day and Whalen (2003). Rare cyrtospiriferines appear during the later part of Early Frasnian time in South Timan (*Echinospirifer*? *distinctus* Ljaschenko, 1973) and in the Main Devonian Field (*Cyrtospirifer tschudovi* Nalivkin, 1941).

Faunal turnover increased significantly at the end of the Early Frasnian that was a period of sea-level low stand, succeeded by the sea level rise during the transgressive phase of T-R cycle IIc at the beginning of the mid-Frasnian (Johnson et al. 1985). It was the time of remarkable proliferation of *Cyrtospitifer* that spread across the whole East European Platform with the exception of the South Timan region, where anoxic and hypoxic environments ("Domanik" lithofacies) predominated at that time, and initial migration of cyrtospiriferines into North American carbonate platforms (Ma and Day 2000, 2003). This interval corresponds to the Semiluki Horizon (Fig. 2, *Pa. punctata–Pa. jamieae* zones; see Ziegler et al. 2000). Proliferation and diversification of new brachiopod associations might have been in a part a reflection of increasing diversity of lithofacies at that time (Rodionova et al. 1995). In the north-western and central regions of European Russia, as well as in the Middle Timan, *Cyrtospirifer* assumed a dominant position within the mid-Frasnian brachiopod associations. In particular, *Cyrtospirifer schelonicus* Nalivkin, 1941 and *Cyrtospirifer tenticulum* (Verneuil, 1845) occur in the north-western region (Main Devonian Field) as characteristic high density associations together with various atrypids, athyridids, and very scarce rhynchonellids (Sokiran 2002; Zhuravlev et al. 2006). In the central region (Fig. 1) *Cyrtospirifer rudkinensis* Ljaschenko, 1959, *Cyrtospirifer* "*disjunctus*" (Sowerby,

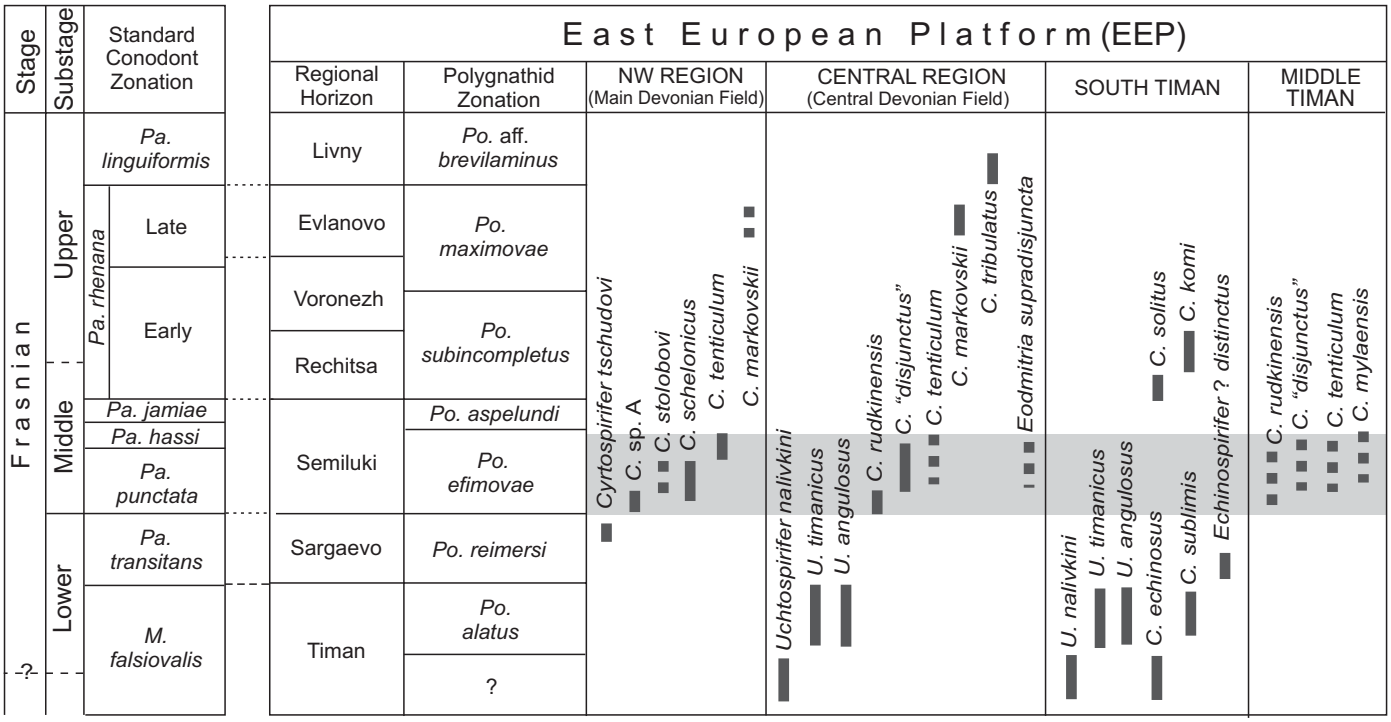

Fig. 2. Distribution of Cyrtospiriferidae in the Frasnian of the East European Platform (EEP). The standard conodont zonation after Klapper and Ziegler (1979), Ziegler and Sandberg (1990), and polygnathid zonation for Frasnian of the EEP proposed by Ziegler et al. (2000). Abbreviations: *C*., *Cyrtospirifer*; *M*., *Mesotaxis*; *Pa*., *Palmatolepis*; *Po*., *Polygnathus*; *U*., *Uchtospirifer*.

1840) (the name of the Russian form is given in parenthesis because it is not conspecific with the Sowerby's species and will be revised elsewhere), *Cyrtospirifer tenticulum*, and *Eodmitria supradisjuncta* (Obrouchev, 1916) are the most characteristic. They co-occur with orthids, strophomenids, early productids, rhynchonellids, atrypids and athyridids (Ljaschenko 1959).

The character of sedimentation and brachiopod associations in the Middle Timan during the Early and Middle Frasnian show, in general, patterns similar to those of the north-western and central regions of the European Russia (Fig. 2). The Early Frasnian Yst'yarega Formation and the Middle Frasnian Kraipol Formation are characterized by a mixture of carbonate and siliciclastic sediments that yield similar brachiopod faunas. In that region *Cyrtospirifer* makes its first appearance in the Kraipol Formation where it is represented by abundant *C. rudkinensis*, *C. mylaensis* sp. nov., *C.* "*disjunctus*", and *C. tenticulum* (Fig. 2). Associated brachiopods include strophomenids, atrypids and rhynchonellids (Tsaplin and Sorokin 1988).

Systematic paleontology

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Cyrtospiriferoidea Termier and Termier, 1949

Family Cyrtospiriferidae Termier and Termier, 1949
Subfamily Uchtospiriferinae Ljaschenko, 1973

[*nom. transl*. Carter et al. 1994: 335 (*ex* Uchtospiriferidae Ljaschenko, 1973: 87)]

Emended diagnosis.—Cyrtospiriferidae with short hinge line and rounded cardinal extremities; deltidium without penetrating foramen; triangular pedicle opening at the base of delthyrium; radial ornament costate with flattened costae separated by narrow interspaces; costae on dorsal fold and ventral sulcus variably developed or absent; micro-ornament with distinct sub-radial capillae converging anteriorly on top of costae, and tubercles; delthyrial plate variably developed. Differs from Cyrtospiriferinae by having a narrow interarea and rounded cardinal extremities. From Cyrtiopsinae differs by having a rounded cardinal extremities, non-perforate deltidium and variably developed delthyrial plate (emended after Ljaschenko 1972).

Remarks.—Carter at al. (1994) considered the Family Uchtospiriferidae Ljaschenko, 1973 as a junior synonym of the Subfamily Cyrtiopsinae Ivanova, 1972 that was recognized as Cyrtospiriferidae with a narrow interarea and rounded cardinal extremities. This point of view was followed by Oleneva (2003, 2004) and Johnson (2006). However, according to Ma and Day (1999) the type species of *Cyrtiopsis* Grabau, 1923, i.e., *Cyrtiopsis davidsoni* Grabau, 1923 has acute cardinal extremities, deltidium penetrated by a foramen close to the apex, and lacks a delthyrial plate. Thus, there is inconsistency in description of cardinal extremities in diagnosis of

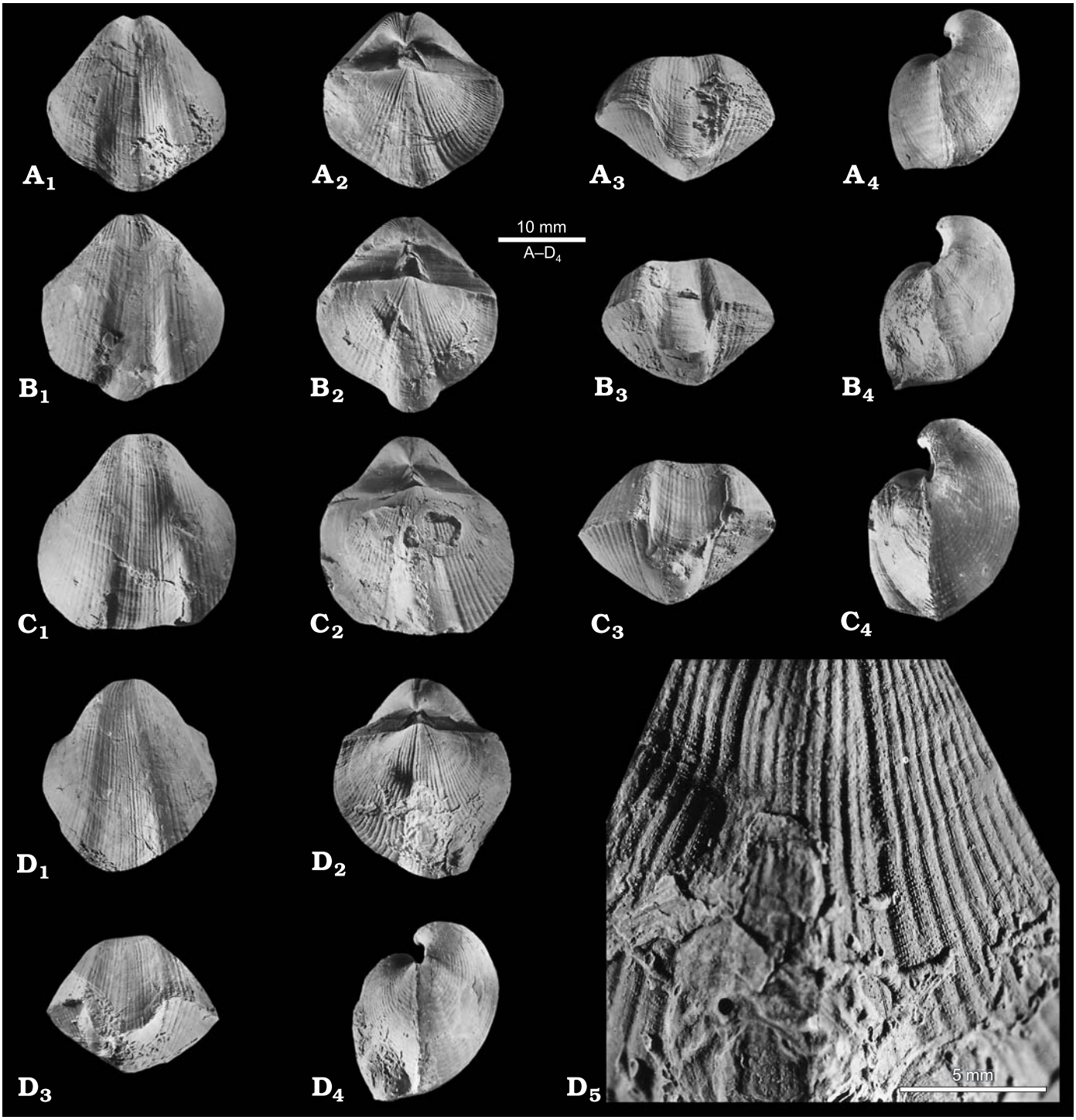

Fig. 3. Early Frasnian cyrtospiriferd *Uchtospirifer nalivkini* Ljaschenko, 1957 from the Kyn Horizon, Urals. **A**. CNIGR 287, ventral (A_1), dorsal (A_2), anterior (A_3), and lateral (A_4) views. **B**. CNIGR 286, ventral (B_1), dorsal (B_2), anterior (B_3), and lateral (B_4) views. **C**. CNIGR 289, ventral (C_1), dorsal (C_2), anterior (C_3), and lateral (C_4) views. **D**. CNIGR 290, ventral (D_1), dorsal (D_2), anterior (D_3), and lateral (D_4) views; shell surface showing microornament (D_5).

Cyrtiopsinae given by Johnson (2006) and *Cyrtiopsis davidsoni* in Ma and Day (1999). Because of that uncertainty and differences between *Uchtospirifer* and *Cyrtiopsis*, we here consider Uchtospiriferinae as a separate taxon within the family Cyrtospiriferidae.

Genera assigned.—*Uchtospirifer* Ljaschenko, 1957.

Genus *Uchtospirifer* Ljaschenko, 1957

1957 *Uchtospirifer* Ljaschenko gen. nov.; Ljaschenko 1957: 885.
1958 *Uchtospirifer* Ljaschenko, 1957; Ljaschenko 1958: 148.
1959 *Uchtospirifer* Ljaschenko, 1957; Ljaschenko 1959: 247.
1973 *Uchtospirifer* Ljaschenko, 1957; Ljaschenko 1973: 88.
1973 *Timanospirifer* Ljaschenko gen. nov.; Ljaschenko 1973: 92.

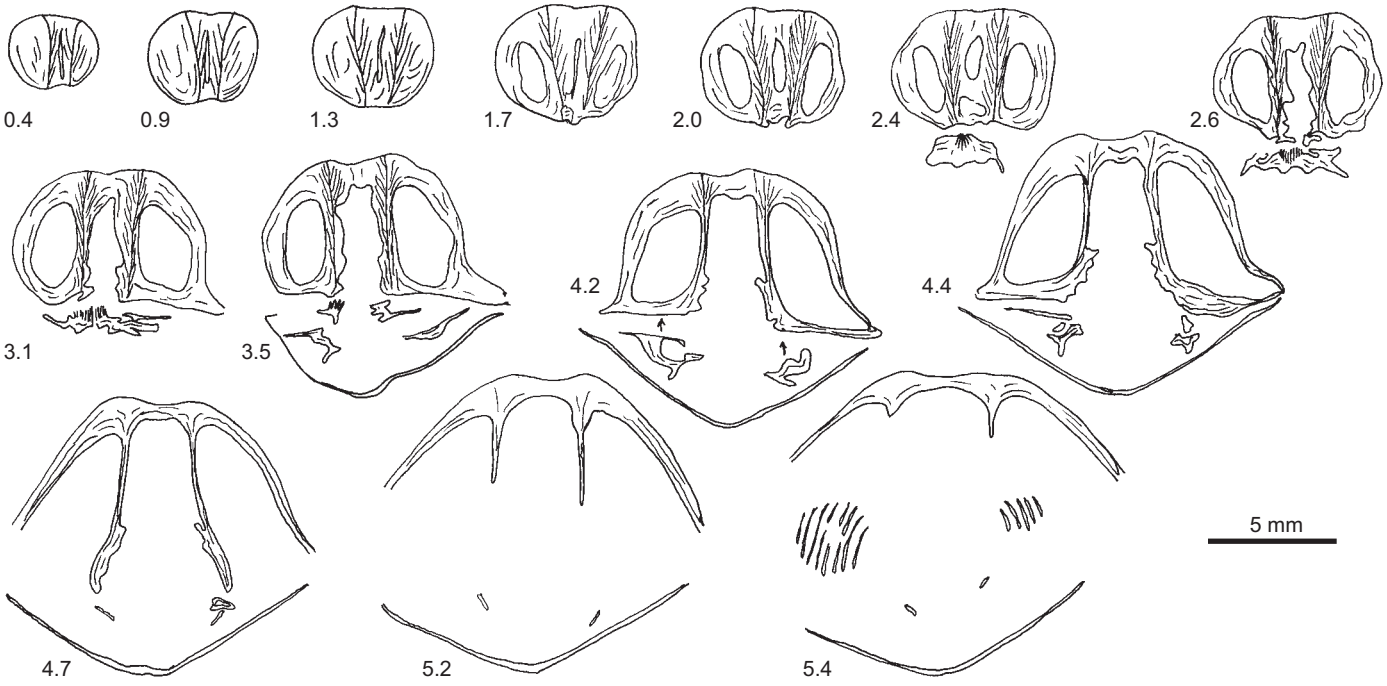

Fig. 4. Transverse serial sections of complete shell of *Uchtospirifer nalivkini* Ljaschenko, 1957, Early Frasnian, Kyn Horizon, Urals. Numbers refer to distances in mm from the top of the ventral umbo, CNIGR 1/13157.

1973 *Nordispirifer* Ljaschenko gen. nov.; Ljaschenko 1973: 104.
1973 *Clivospirifer* Ljaschenko gen. nov.; Ljaschenko 1973: 108.
1973 *Acutella* Ljaschenko gen. nov.; Ljaschenko 1973: 119.

Emended diagnosis.—Moderately to strongly inflated shells with short hinge and rounded cardinal extremities; delthyrium covered by deltidium except for triangular opening at the base of delthyrium; dorsal fold and ventral sulcus variably developed; costate ornamentation with closely spaced and flattened costae; costae on fold and sulcus variably developed or absent; micro-ornamentation consists of sub-radial capillae converging on top of costae and tubercles; ventral interior with dental plates, with or without delthyrial plate. Differs from *Cyrtospirifer* by short hinge, rounded cardinal extremities, and micro-ornamentation (emended after Ljaschenko 1957, 1959, 1972).

Remarks.—The number of spiriferid taxa described by Ljaschenko (1959, 1973) from the Devonian of South Timan was reduced considerably after substantial revisions by Talent and Gratsianova (1988) and Oleneva (2003, 2004). In particular the genera *Timanospirifer*, *Nordispirifer*, *Clivospirifer*, and *Acutella* were reassigned as junior synonyms of *Uchtospirifer* because of similar shell morphology and micro-ornamentation.

Talent and Gratsianova (1988) considered *Mennespirifer* as synonym of *Cyrtospirifer*. Recently Oleneva (2006) recognized *Mennespirifer* as a junior synonym of *Komispirifer* although Ljaschenko (1959, 1973) considered the former as belonging to uchtospiriferins.

The diagnostic external characters of uchtospiriferins include rounded cardinal extremities and peculiar micro-ornamentation (see Ljaschenko 1973; Oleneva 2003, 2004). Noteworthy is also a weakening or complete disappearance of sinal costae in some representatives of the subfamily (e.g., in *Uchtospirifer angulosus*, *U. timanicus*, and *U. nalivkini*). These characters distinguish them from *Cyrtospirifer* and *Cyrtiopsis*. Moreover, the latter have foramen at the top of the deltidium. Therefore, Ljaschenko (1973) distinguished uchtospiriferines from other Cyrtospiriferidae.

Uchtospirifer nalivkini Ljaschenko, 1957

Figs. 3, 4.

1845 *Spirifer Murchisonianus* de Koninck (ined.); Verneuil: 160, pl. 4: 1.
1887 *Cyrtia murchisoniana* (de Koninck); Chernyshev 1887: 77, pl. 13: 3–7.
1947 *Cyrtospirifer murchisonianus* (de Koninck); Nalivkin 1947: 116, pl. 27: 8.
1957 *Uchtospirifer nalivkini* sp. nov.; Ljaschenko 1957: 886, pl. 1: 1–4.
1958 *Uchtospirifer nalivkini* Ljaschenko, 1957; Ljaschenko 1958: 148, pl. 11: 1–3.
1959 *Uchtospirifer nalivkini* Ljaschenko, 1957; Ljaschenko 1959: 122, pl. 14: 1–9.
1973 *Uchtospirifer nalivkini* Ljaschenko, 1957; Ljaschenko 1973: 88, pl. 27: 1–7, pl. 51: 2.
1969 *Uchtospirifer solnzevi* sp. nov.; Ljaschenko 1969: 50, pl. 10: 2.
1969 *Uchtospirifer concentricus* sp. nov.; Ljaschenko 1969: 51, pl. 10: 1.
1973 *Uchtospirifer concentricus* Ljaschenko, 1969; Ljaschenko 1973: 91, pl. 28: 1, pl. 52: 1.

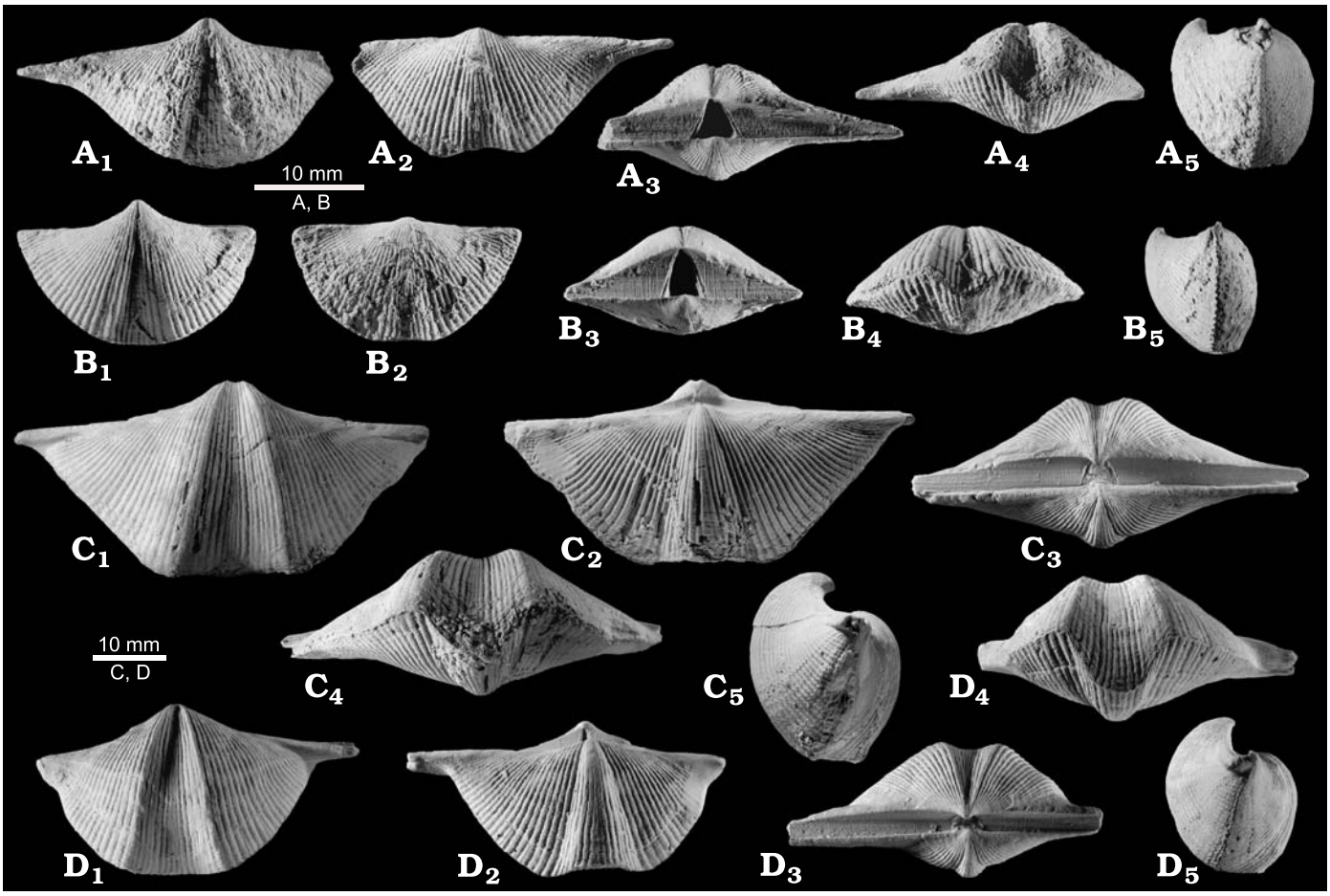

Fig. 5. Cyrtospiriferids from Middle Frasnian of the Main and Central Devonian Fields. **A**, **B**. *Cyrtospirifer schelonicus* (Nalivkin, 1941), Svinord Beds, Main Devonian Field. **A**. CNIGR 2/13157, ventral (A_1), dorsal (A_2), posterior (A_3), anterior (A_4), and lateral (A_5) views. **B**. CNIGR 3/13157, ventral (B_1), dorsal (B_2), posterior (B_3), anterior (B_4), and lateral (B_5) views. **C**, **D**. *Cyrtospirifer rudkinensis* Ljaschenko, 1959, Semiluki Horizon, Central Devonian Field. **C**. CNIGR 4/13157 ventral (C_1), dorsal (C_2), posterior (C_3), anterior (C_4), and lateral (C_5) views. **D**. CNIGR 5/13157 ventral (D_1), dorsal (D_2), posterior (D_3), anterior (D_4), and lateral (D_5) views.

1973 *Uchtospirifer solnzevi* Ljaschenko, 1969; Ljaschenko 1973: 90, pl. 28: 2, 3.

?1981 *Uchtospirifer nalivkini* Ljaschenko, 1957; Racki and Baliński 1981: 202, pl. 10: 1–5.

2003 *Uchtospirifer nalivkini* Ljaschenko, 1957; Oleneva 2003: 27, pl. 1: 3, 5, pl. 2: 3, pl. 16: 4, pl. 17: 5, pl. 18: 3, 5, 6.

2004 *Uchtospirifer nalivkini* Ljaschenko, 1957; Oleneva 2004: 178, pl. 7: 1, 8, 9, pl. 8: 1, 3.

Material.—Seventy six complete shells from George Frederik's collection; the specimens were found at Kyn village in the Urals.

Remarks.—Racki and Balinski (1981) described *Uchtospirifer nalivkini* from the Late Givetian deposits of Góra Zamkowa at Chęciny, Holy Cross Mountains. The Polish specimens seem to be close internally and externally to *U. nalivkini* from Timan, although the micro-ornamentation of the former is not preserved.

Occurrence.—Late Givetian?–Early Frasnian, *Mesotaxis falsiovalis* Zone, Timan Horizon, Central Devonian Field, South Timan, and Kyn Horizon of the Urals and possibly Late Givetian of the Holy Cross Mountains, Poland.

Subfamily Cyrtospiriferinae Termier and Termier, 1949

Genus *Cyrtospirifer* Nalivkin in Frederiks, 1924

Cyrtospirifer schelonicus Nalivkin, 1941

Figs. 5A, B, 6, 10G, H.

1886 *Spirifer Verneuili* Murchison, 1840; Venyukov 1886: 64–79, pl. 4: 4.

1886 *Spirifer Archiaci* Murchison, 1840; Venyukov 1886: 64–79, pl. 4: 1.

1916 *Spirifer verneuili* Murchison, 1840; Obrouchev 1916, pl. 2: 22, 23.

1941 *Cyrtospirifer schelonicus* sp. nov.; Nalivkin 1941: 178, pl. 6: 1–5.

1947 *Cyrtospirifer schelonicus* Nalivkin, 1941; Nalivkin 1947: 113, pl. 27: 1, 2.

Material.—Twenty four well preserved complete shells and eight disarticulated valves collected by Roman F. Hecker near Koloschka river, NW of EEP and in addition three complete shells recently collected.

Remarks.—According to the original description by Nalivkin (1941) *Cyrtospirifer schelonicus* is a morphologically variable species that includes the shells formerly described from the Svinord Beds of the Main Devonian Field by Venyukov

(1886) under the names *Spirifer archiaci*, *Spirifer verneuili*, and *Spirifer tenticulum*. Nalivkin (1941) recognized several morphotypes within the species: (1) transverse, subtrapezoidal shells with a high triangular ventral interarea superficially similar to *Cyrtospirifer verneuili* (Murchison, 1840); (2) shells similar to *C. disjunctus* (Sowerby, 1840), and (3) transverse shells with a subpyramidal ventral valve, a broad ventral interarea and a low dorsal median fold seemingly comparable to *C. tenticulum* (Verneuil, 1845). The species, however, can be easily distinguished from *C. verneuili* (Murchison, 1840) in having less numerous costae, more concave and wider ventral interarea and a lower dorsal median fold.

Brice (1970) described *Cyrtospirifer schelonicus* from the Middle Frasnian of Afghanistan (Ghouk region). Four shells illustrated by her (Brice 1971: 128–132, pl. 7: 1–4) show great variability in general shell outline and convexity, shape of the cardinal extremities, and development of the ventral interarea. However, one of those shells (i.e., Brice 1970: pl. 7: 3) seems to be close to *C. schelonicus* from the Main Devonian field.

Occurrence.—Middle Frasnian, *Palmatolepis punctata–Pa. hassi* zones, Svinord and Il'men Beds, Main Devonian Field.

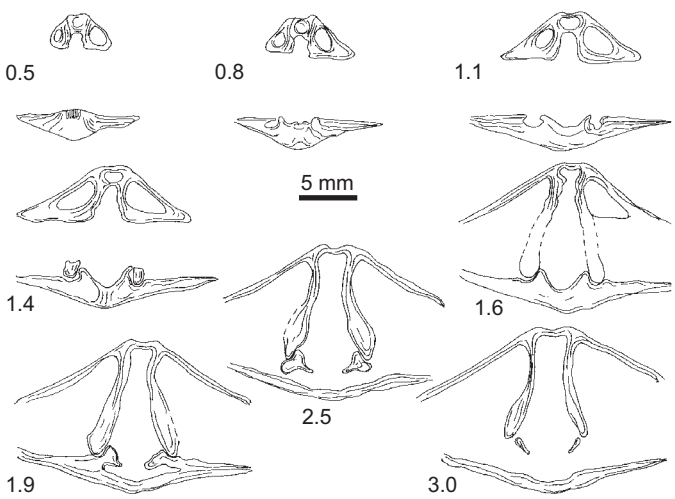

Fig. 6. Transverse serial sections of complete shell of *Cyrtospirifer schelonicus* (Nalivkin, 1941), Middle Frasnian, Svinord Beds, Main Devonian Field. CNIGR 6/13157. Distance in mm is measured from the posterior tip of ventral beak.

Cyrtospirifer rudkinensis Ljaschenko, 1959

Figs. 5C, D, 7.

1959 *Cyrtospirifer rudkinensis* sp. nov.; Ljashenko 1959: 161, pl. 39: 1–4, pl. 40: 2, 3.

Material.—Fifty well preserved and eight flattened shells collected by the author from Rudkino village, Don river, Central Devonian Field, and 61 complete shells from Tsylma, Pizhma Pechorskaya and Myla rivers, Middle Timan from Feodosij N. Chernyshev's collection.

Remarks.—This species differs from *Cyrtospirifer schelonicus* Nalivkin, 1941 in having a more inflated ventral valve with a lower interarea, narrower delthyrium, wider umbo with a strongly curved beak, and coarser ribs. *C. rudkinensis* differs from similar *C. placitus* Stainbrook, 1945 in having generally more swollen umbo and more straight lateral margins.

Occurrence.—Middle Frasnian, *Palmatolepis punctata–Pa. jamieae* zones, Semiluki Horizon, Central Devonian Field; Kraipol Formation, Middle Timan.

Cyrtospirifer mylaensis sp. nov.

Figs. 8, 9.

Holotype: CNIGR 8/13157, complete shell; Fig. 8A.

Type locality: Myla river, Middle Timan.

Type horizon: Kraipol Formation.

Derivation of the name: from Myla river, Middle Timan.

Diagnosis.—Medium sized subtrapezoidal in outline *Cyrtospirifer* with extended cardinal extremities, moderately high apsacline ventral interarea and well defined ventral sulcus. Differs from close *C. schelonicus* in having weakly marked to almost absent dorsal median fold sometimes with shallow medial depression.

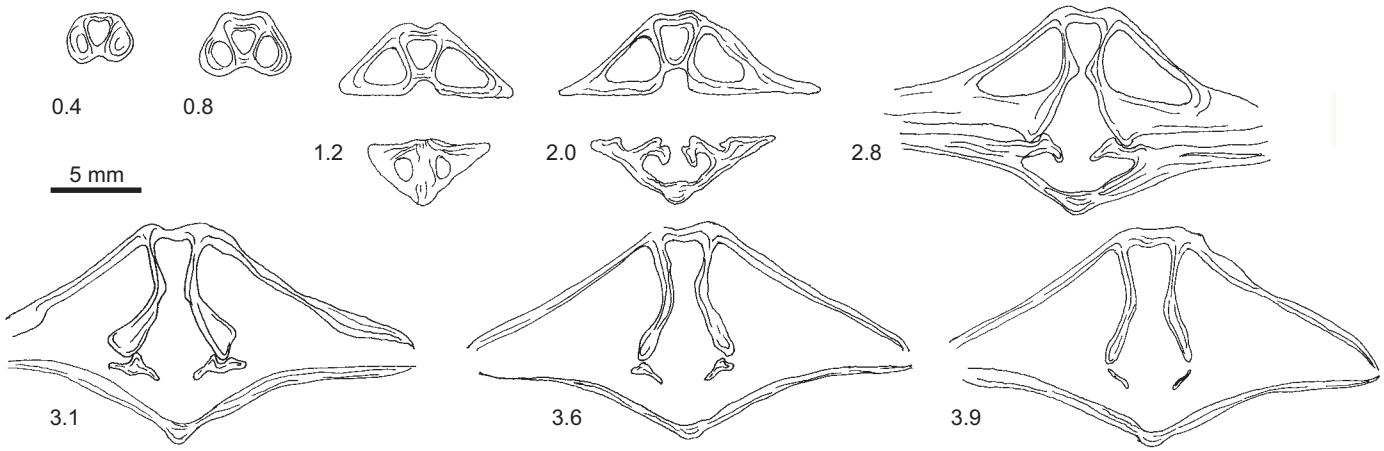

Fig. 7. Transverse serial sections of complete shell of *Cyrtospirifer rudkinensis* (Ljaschenko, 1959), Middle Frasnian, Semiluki Horizon, Central Devonian Field. CNIGR 7/13157. Distance in mm is measured from the posterior tip of ventral beak.

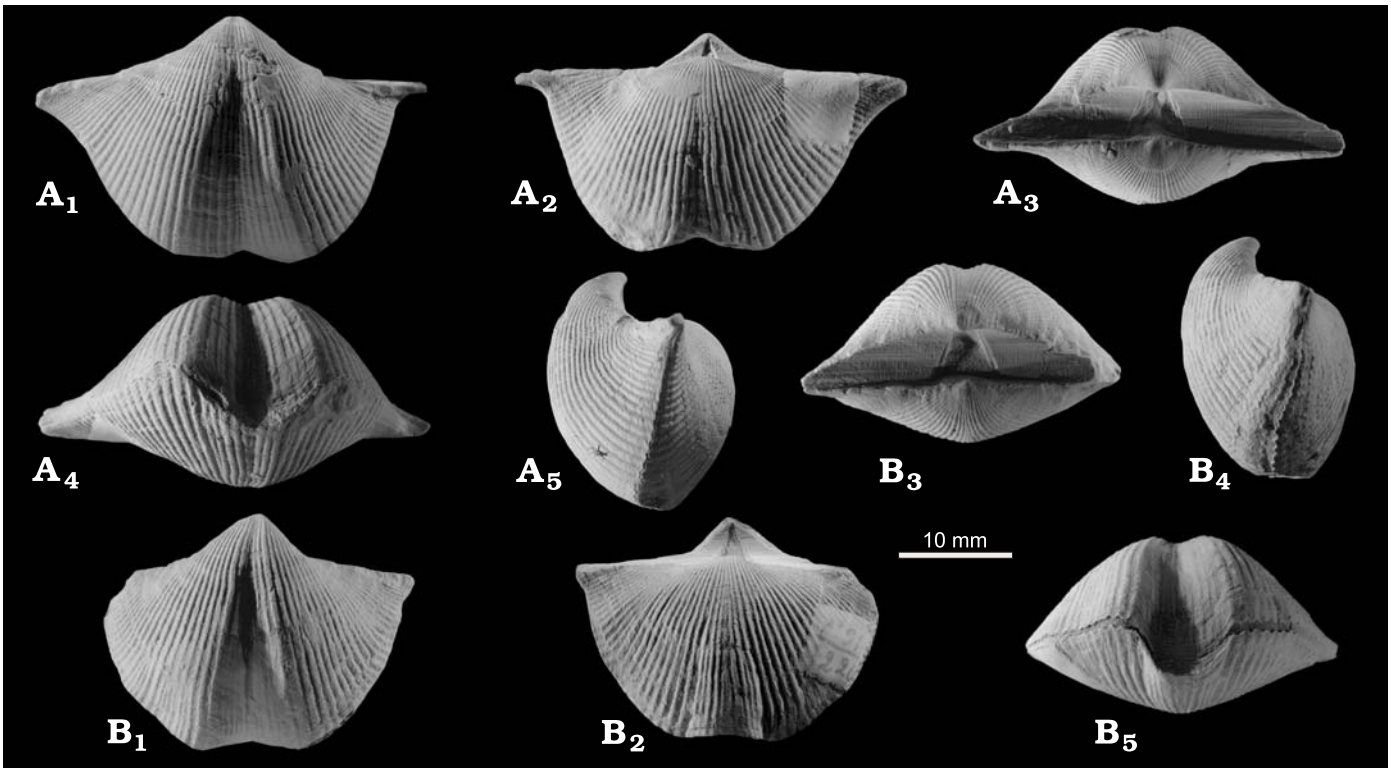

Fig. 8. *Cyrtospirifer mylaensis* sp. nov., Middle Frasnian, Kraipol Formation, Middle Timan. **A**. Holotype, CNIGR 8/13157, ventral (A_1), dorsal (A_2), posterior (A_3), anterior (A_4), and lateral (A_5) views. **B**. CNIGR 9/13157, ventral (B_1), dorsal (B_2), posterior (B_3), anterior (B_4), and lateral (B_5) views.

Material.—More than 100 well preserved specimens collected by Feodosij N. Chernyshev (Myla and Pizhma Pechorskaya rivers, Middle Timan); in addition six well preserved complete and six exfoliated shells recently collected from Pizhma Pechorskaya river.

Description.—Shell ventribiconvex, medium sized (up to 35 mm wide) transverse subtrapezoidal in outline, with maximum width at hinge line; cardinal extremities acute and alate; anterior commissure uniplicate. Ventral valve moderately to strongly convex with a small slightly curved beak; ventral interarea high, up to 8.4 mm in adult specimens, strongly apsacline; delthyrium triangular attaining 4.9–7.9 mm in width. Sulcus well defined, originates at the umbo, terminates with a low and rounded tongue. Dorsal valve moderately convex, slightly shallower than ventral valve. Dorsal median fold weakly developed to almost absent, sometimes with a shallow medial depression. Radial ornament with up to 24 simple low ribs separated by narrow interspaces on each flank. Ventral sulcus and dorsal median fold with up to 13 bifurcating ribs along the anterior margin. Microornament of fine radial capillae and fine concentric filae.

Ventral interior with a delthyrial plate, simple strong teeth, and long, divergent extrasinal dental plates. Dorsal interior with a ctenophoridium; a low median ridge present.

Remarks.—The main diagnostic future of *Cyrtospirifer mylaensis* is the absence or weak development of dorsal fold with shallow medial depression. However, the low dorsal fold is also characteristic for some specimens of *C.* "*disjunctus*" from Russia (*sensu* Verneuil 1845) and *C. tenticulum* (Verneuil, 1845). *C. mylaensis* differs from *C.* "*disjunctus*" in having more trapezoidal shell outline and higher, triangular ventral interarea which in the latter has its lateral edges nearly parallel to the hinge line. From *C. tenticulum* the new species differs by its larger shell and lower, not pyramidal ventral interarea. The median depression or longitudinal groove on the dorsal fold occurs also in *C. bisellatus* (Gürich, 1903) and *C. bisinus* (Le Hon, 1870), but this is more distinct than that in *C. mylaensis*. In addition *C. mylaensis* differs from *C. bisinus* by having higher, more triangular ventral interarea. From *C. bisellatus* the new species differs in its more trapezoidal, not pentagonal shell outline and in having greatest shell width at its hinge line whereas the former is widest usually at the shell midlength.

Occurrence.—Middle Frasnian, *Palmatolepis punctata–Pa. jamieae* zones, Kraipol Formation, Middle Timan.

Cyrtospirifer tenticulum (Verneuil, 1845)

Figs. 10 A, B, 11, 12.

1845 *Spirifer tenticulum* sp. nov.; Verneuil in Verneuil, Murchison, and Keyserling 1845: 159, pl. 5: 7.

1930 *Spirifer* (*Cyrtospirifer*) *tenticulum* (Verneuil 1845); Nalivkin 1930: 76, pl. 7: 4, 8, 9.

1941 *Cyrtospirifer tenticulum* (Verneuil 1845); Nalivkin 1941: 180, pl. 7: 3–5.

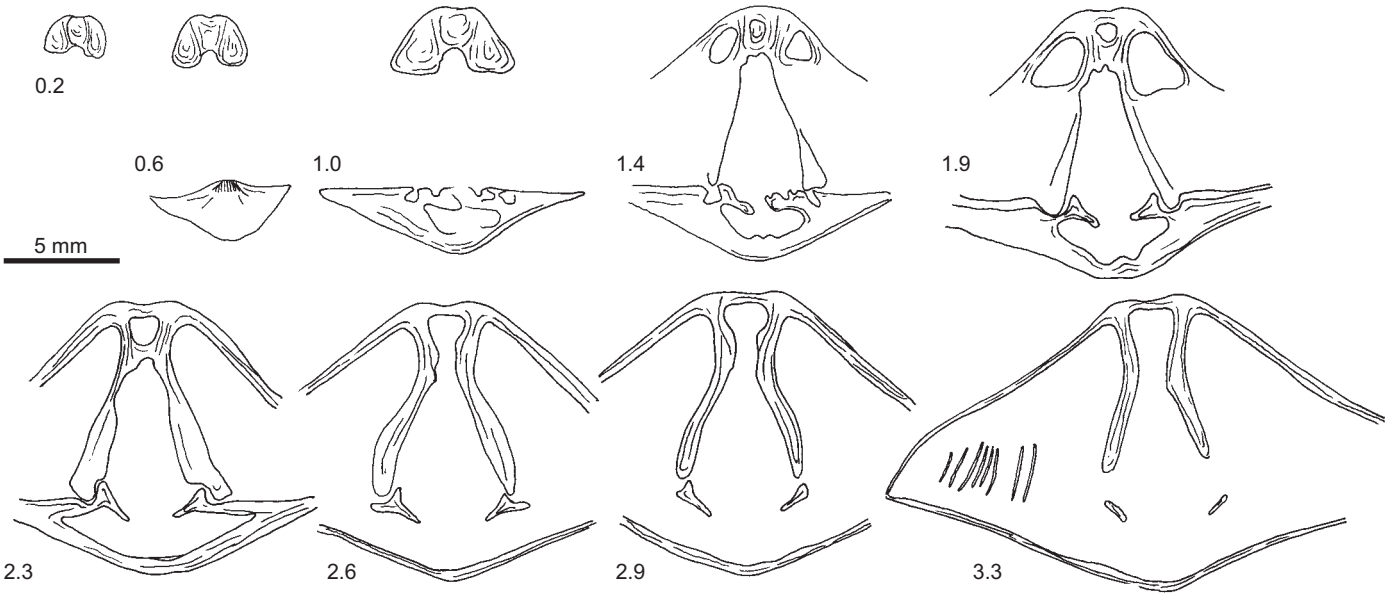

Fig. 9. Transverse serial sections of complete shell of *Cyrtospirifer mylaensis* sp. nov., from Middle Frasnian, Kraipol Formation, Middle Timan. CNIGR 10/13157. Distance in mm is measured from the posterior tip of ventral beak.

1947 *Cyrtospirifer tenticulum* (Verneuil 1845); Nalivkin 1947: 115, pl. 27: 5, 6.

2000 *Tenticospirifer tenticulum* (Verneuil 1845); Ma and Day 2000: 451, fig. 3, 4.1–4.3, 4.5, 5.1–5.3.

Neotype: Complete shell CNIGR 93/6993 designed herein, illustrated in Nalivkin (1941: pl. 7: 5) and re-illustrated here in Fig. 10A.

Material.—Twelve complete shells and one ventral valve from Roman F. Hecker's collection (Il'men lake region) and twenty nine ventral and seven dorsal valves recently collected from the Psizha river banks and old quarry near Buregi village (Il'men lake region, Main Devonian Field).

Remarks.—Nalivkin (1977) noted that type specimens of several species described by Verneuil (1845) and deposited in the l'Ecole Nationale Superieure des Mines de Paris are partly lost as is the case with types of *Spirifer tenticulum*. Therefore, the neotype of *Cyrtospirifer tenticulum* is selected here to resolve some uncertainties in affinities and taxonomy of the species (Fig. 10A).

Tien (1938) selected *Spirifer tenticulum* Verneuil, 1845, as the type species of *Tenticospirifer*. Subsequently most of researchers (Paeckelmann 1942; Rzhonsnitskaya 1952; Vandercammen 1959; Sidjachenko 1962; Talent and Gratsianova 1986; Alekseeva et al. 1996) considered this taxon as junior synonym of *Cyrtospirifer*. Beznosova (1959), Ljaschenko (1959), Bublichenko (1971, 1974), Ma and Day (2000), and Johnson (2006) regarded *Tenticospirifer* as valid taxon. In the last comprehensive revision of the Family Cyrtospiriferidae published by Ma and Day (2000) *Tenticospirifer* was defined as having a subpyramidal ventral valve with catacline to slightly procline interarea, narrow delthyrium, short delthyrial plate, in-filled notothyrial cavity of the dorsal valve by secondary shell material, lacking a myophragm bisecting dorsal muscle field, smaller numbers of ribs in the ventral sulcus and on the dorsal fold. In addition *Cyrtospirifer lictor* Nalivkin, 1930 from the Middle Frasnian of central Russia and some other species from North America and Europe were assigned by these authors to *Tenticospirifer*.

However, observations on individual and ontogenetic changes in several species of *Cyrtospirifer* from the Main Devonian Field and Central Devonian Field suggest that most of listed diagnostic features are in a fact present in various species of *Cyrtospirifer* and sometime their expression is a matter of intraspecific variation. In particular, the juvenile shells of *Cyrtospirifer tenticulum* have 4 ribs in sulcus whereas in the adult specimens this number increases up to 9. By comparison, *Cyrtospirifer schelonicus* has 7 to 14 ribs in the sulcus. *Cyrtospirifer lictor* that was assigned to *Tenticospirifer* by Ma and Day (2000) has up to 14 ribs in the sulcus. The specimen of *Tenticospirifer tenticulum* (unfortunately without precise geographical location) illustrated in the recently revised Treatise (Johnson 2006: 1729, fig 1133: 3) has 16–17 sinal ribs, while here selected neotype has eight ribs. A notothyrial cavity filled with secondary shell can be observed in gerontic shells of *Cyrtospirifer schelonicus* (Fig. 6). Inclination of the ventral interarea in *Cyrtospirifer tenticulum* varies from catacline to apsacline (see Nalivkin 1930: pl. 7: 4, 8, 9; Nalivkin 1941: pl. 7: 3–5) whereas in *Cyrtospirifer lictor* it can be slightly apsacline (see Nalivkin 1930: pl. 7: 5). By contrast, some populations of *Cyrtospirifer schelonicus* include specimens with a catacline ventral interarea (Fig. 10H) and a subpyramidal ventral valve. Thus, we prefer to follow the opinion of those authors who regard *Tenticospirifer* as a synonym of *Cyrtospirifer*.

Cyrtospirifer tenticulum differs from the type species of *Cyrtospirifer*, i.e., *C. verneuili*, in having pyramidal ventral valve and less numerous sinal and lateral plications.

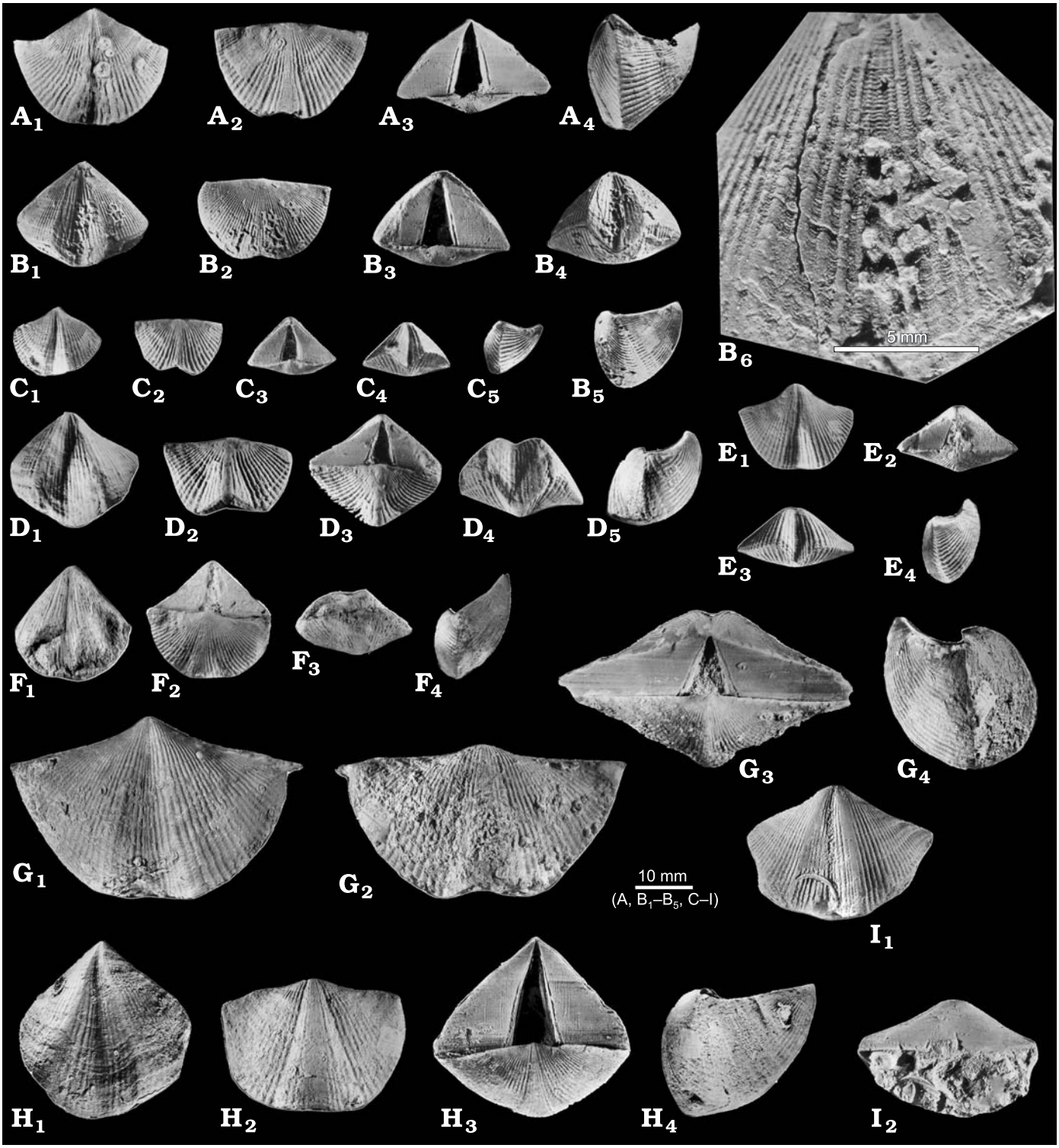

Fig. 10. Cyrtospiriferids from Middle Frasnian of the Main and Central Devonian Fields. **A–C**. *Cyrtospirifer tenticulum* (Verneuil, 1845). **A**. Buregi Beds, Main Devonian Field. CNIGR 93/6993, neotype, ventral (A_1), dorsal (A_2), posterior (A_3), and lateral (A_4) views. **B**, **C** Semiluki Horizon, Central Devonian Field. **B**. CNIGR 3535/2858, ventral (B_1), dorsal (B_2), posterior (B_3), anterior (B_4), and lateral (B_5) views, and shell surface showing microornament (B_6). **C**. CNIGR 3534/2858, ventral (C_1), dorsal (C_2), posterior (C_3), anterior (C_4), and lateral (C_5) views. **D**, **E**. *Cyrtospirifer lictor* Nalivkin, 1930, Semiluki Horizon, Don river, Central Devonian Field. **D**. CNIGR 3530/2858, ventral (D_1), dorsal (D_2), posterior (D_3), anterior (D_4), and lateral (D_5) views. **E**. CNIGR 3531/2858, ventral (E_1), posterior (E_2), anterior (E_3), and lateral (E_4) views. **F**. *Cyrtospirifer* sp. A, Porkhov Beds, Main Devonian Field. CNIGR 11/13157, ventral (F_1), posterior (F_2), anterior (F_3), and lateral (F_4) views. **G**, **H**. *Cyrtospirifer schelonicus* (Nalivkin, 1941), Svinord Beds, Main Devonian Field. **G**. CNIGR 88/6993, ventral (G_1), dorsal (G_2), posterior (G_3), and lateral (G_4) views. **H**. CNIGR 87/6993, ventral (H_1), dorsal (H_2), posterior (H_3), and lateral (H_4) views. **I**. *Cyrtospirifer tschudovi* Nalivkin, 1941, Chudovo Beds, Main Devonian Field, CNIGR 1/6993, ventral (I_1) and posterior (I_2) views.

Occurrence.—Middle Frasnian, *Palmatolepis punctata–Pa. hassi* zones, Buregi Beds, Main Devonian Field, Semiluki Horizon, Central Devonian Field, Kraipol Formation, Middle Timan.

Cyrtospirifer sp. A

Fig. 10F.

Material.—Two complete shells and ten incomplete single valves collected from Schelon' river basin.

Description.—Shell small sized (up to 20 mm in width) with maximum width at hinge line; cardinal extremities acute and short; anterior commissure uniplicate. Pyramidal ventral valve weakly convex with a small slightly curved beak; ventral interarea catacline to apsacline. Sulcus shallow originates at the umbo. Dorsal valve moderately convex with weakly developed fold. Radial ornament with up to 18 simple low ribs separated by narrow interspaces on each flank. Ventral sulcus and dorsal fold with up to 9 bifurcating ribs along the anterior margin.

Ventral interior with a delthyrial plate and divergent extrasinal dental plates. Dorsal interior with a ctenophoridium.

Remarks.—This is small-sized *Cyrtospirifer* with pyramidal ventral valve similar to *Cyrtospirifer tenticulum*. It differs from the latter by more rounded lateral margins and less convex ventral valve.

Cyrtospirifer sp. A is similar to *Tenticospirifer lagovensis* (Gürich, 1896) from the Late Givetian of the Holy Cross Mountains, Poland, but differs in having thinner ribs, narrower and less sharply bounded sulcus and fold. *C*. sp. A is somewhat suggestive of the Late Frasnian North American *Cyrtospirifer pyramidalis* Cooper and Dutro, 1982 but it differs in generally weakly convex ventral valve and finer ribs. Sorokin (1978) listed this form from Porkhov Beds of the Schelon river basin as *Cyrtospirifer schelonicus* var. *tenticula*.

Occurrence.—Middle Frasnian, *Palmatolepis punctata* Zone, Porkhov Beds, Main Devonian Field.

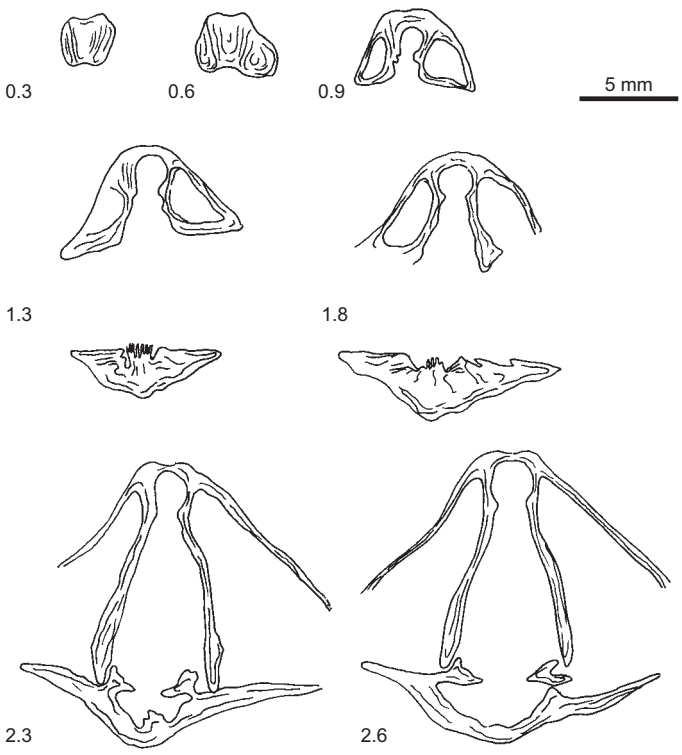

Fig. 11. Transverse serial sections of complete shell of *Cyrtospirifer tenticulum* (Verneuil, 1845), Middle Frasnian, Buregi Beds, Main Devonian Field. CNIGR 12/13157. Distance in mm is measured from the posterior tip of ventral beak.

Discussion

There are several episodes of the increased faunal turnover during the Frasnian suggesting that brachiopod faunas, which inhabited shallow epeiric seas that covered the East European Platform experienced considerable environmental stress. These episodes show distinct correlation with sea-level fluctuations (Fig. 13). A major reorganization of the brachiopod assemblages occurred at the beginning of the

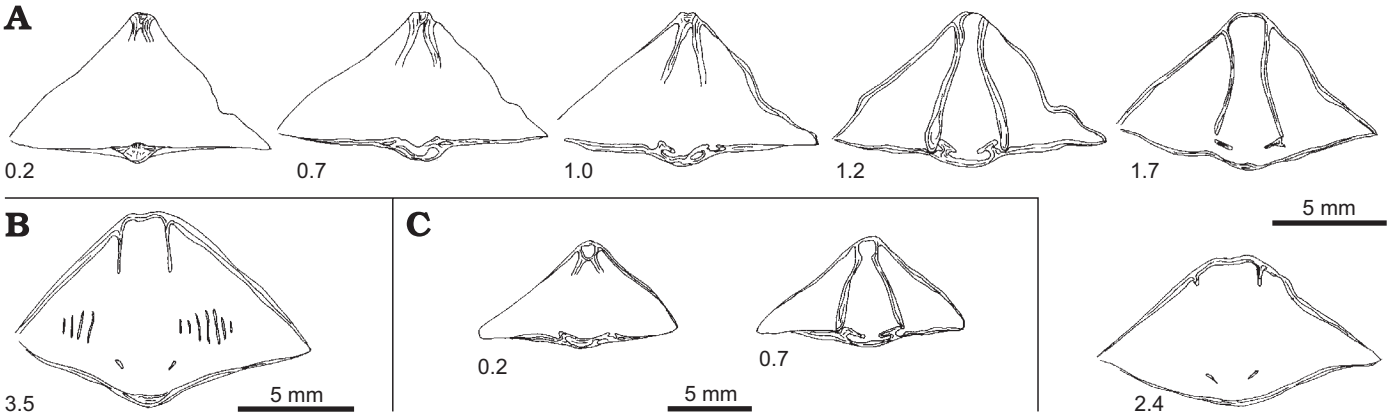

Fig. 12. Transverse serial sections of complete shells of *Cyrtospirifer tenticulum* (Verneuil, 1845), Middle Frasnian, Buregi Beds, Main Devonian Field. **A**. CNIGR 13/13157. **B**. CNIGR 14/13157. **C**. CNIGR 15/13157. Distance in mm is measured from the posterior tip of ventral beak.

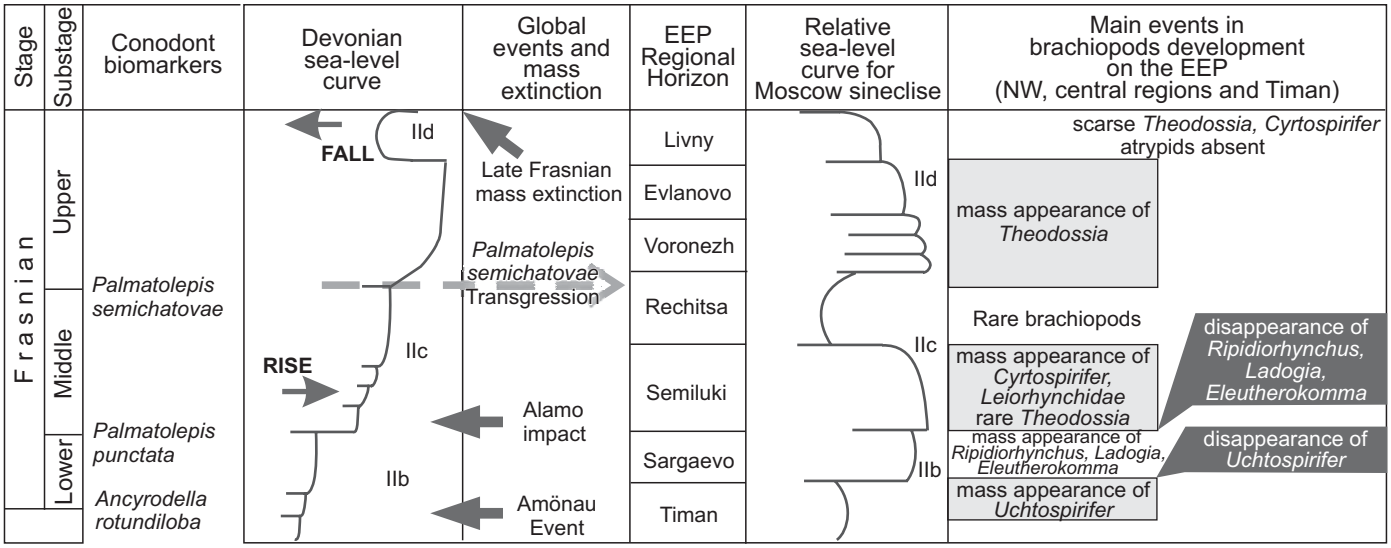

Fig. 13. Main events in brachiopod development on the East European Platform (North-West and central regions, and Timan). Devonian sea-level curve (after Johnson et al. 1985; see Racki 1993) and curve of relative Devonian se-level changes in Moscow Syneclise after Alekseev et al. (1996). Global events and mass extinction after Sandberg et al. (2002).

transgressive phase of transgressive-regressive cycles and it was usually connected with major immigrations of new faunas (Sokiran 1998, 2002). In particular, faunal turnover near the Early to Middle Fransian transition was resulted in complete disappearance of the brachiopod associations dominated by *Ripidiorhynchus*, *Ladogia*, and *Eleutherokomma* (Zhuravlev et al. 2006). The mid-Frasnian transgression coincides with proliferation of *Cyrtospirifer* and appearance of theodossiids.

Observed patterns of a faunal turnover and immigration were probably governed by eustatically controlled sea level fluctuations. Noteworthy, no evidence of correlation with some other important physical events that had occurred during the Late Devonian was revealed. In particular, the Alamo Impact that according to Sandberg et al. (2002) occurred in the middle of the *Palmatolepis punctata* Zone had no effect on the brachiopod faunal dynamics during that time. Significant mid-Frasnian $\delta^{13}C$ excursion is known in Belgium, Poland, and South China (Yans et al. 2006), and Zhuravlev et al. (2006) recorded significant brachiopod and ostracod turnover during the E–MF interval that coincides with the positive $\delta^{13}C$ signal on the EEP.

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